

**BIOLOGY OF THE CIRRATE OCTOPOD *GRIMPOTEUTHIS GLACIALIS*
(CEPHALOPODA; OPISTHOTEUTHIDIDAE) IN THE SOUTH SHETLAND
ISLANDS, ANTARCTICA**

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The capture of 52 specimens of the cirrate octopod *Grimpoteuthis glacialis* (Robson, 1930), of dorsal mantle length 20–165 mm during a 1996 trawling survey near the Antarctic Peninsula allowed the basic biology of the species to be examined. Their presence in bottom trawls at depths of 333–879 m, but their absence from benthopelagic and pelagic trawls, is consistent with a primarily benthic habitat. The largest single sample, 40 animals, came from a soft mud bottom and highlights the patchy nature of the distribution. Males tended to be bigger in total length and mass than females of similar mantle length. The males, however, were mature at a smaller size. Mature males have tiny sperm packets, rather than typical cephalopod spermatophores, in their distal reproductive tract. Mature females have large, smooth eggs in the proximal oviduct, in the huge oviducal gland and in the distal oviduct. Eggs in the distal oviduct have a thick, sticky coating that hardens in seawater into a secondary egg case. Ovarian eggs vary greatly in size, possibly indicating protracted egg laying. Observations on live animals indicate that the species swims primarily by fin action, rather than by jetting or medusoid pulses with the arm/web complex. It may be capable of limited changes in colour pattern, especially on the oral surface of the web. Three pairs of surface structures that appear superficially to be white spots anterior to the eyes and near the bases of the fins are actually transparent patches in the skin. When considered in association with the transparent subdermal layer and the anatomy of the eyes, optic nerves and optic lobes, these clear patches seem to function in detecting unfocused light on the horizontal plane of the benthic animal.

The cirrate, or finned, octopods are deep-sea animals about which little is known. They are rarely seen. Because most species have a gelatinous consistency, specimens collected by trawling generally are in very poor condition (Vecchione 1987). Some recent observations, based either on exceptional specimens from trawling with large nets (Aldred *et al.* 1983, Villanueva and Guerra 1991) or on direct observation from submersibles (Vecchione and Roper 1991, Vecchione and Young 1997), have added substantially to knowledge of a few species. However, the morphology, anatomy, general biology and distribution of most species are poorly known. The capture of 52 specimens of a cirrate species (see taxonomic comments below) during the bottom trawling component of an expedition to the Southern Ocean allowed detailed observations on these basic aspects of the species' biology.

Cirrates are a distinct systematic clade, the sister group to the better-known incirrate octopods (Young and Vecchione 1996). Because of the collection problems mentioned above, cirrate systematics remain problematic (Voss 1988a). The species discussed in the present paper was described by Robson (1930) as *Cirroteuthis glacialis*, but it is known in recent litera-

ture (e.g. Kubodera and Okutani 1986, Voss 1988b, Vecchione and Young 1997) as *Grimpoteuthis glacialis* (Robson, 1930). However, S. O'Shea (National Institute of Water and Atmosphere, Wellington, New Zealand, pers. comm. 1996) is probably correct in asserting that this species is distinct from the genus *Grimpoteuthis sensu strictu*. However, for now it is still referred to as *Grimpoteuthis glacialis* at least until a systematic review of the group is published. In addition, relationships between this species and other Antarctic cirrates is also problematic (O'Shea, pers. comm. 1997). Correct familial assignments for all cirrate octopods must await analysis by modern systematic methods. As Robson (1930) noted, the species seems more robust than most other cirrates because specimens captured in bottom trawls often are in relatively good condition.

MATERIAL AND METHODS

The second leg of R. V. *Polarstern*'s cruise ANT XIV, in November–December 1996, focused on the South Shetland Islands north-west of the Antarctic

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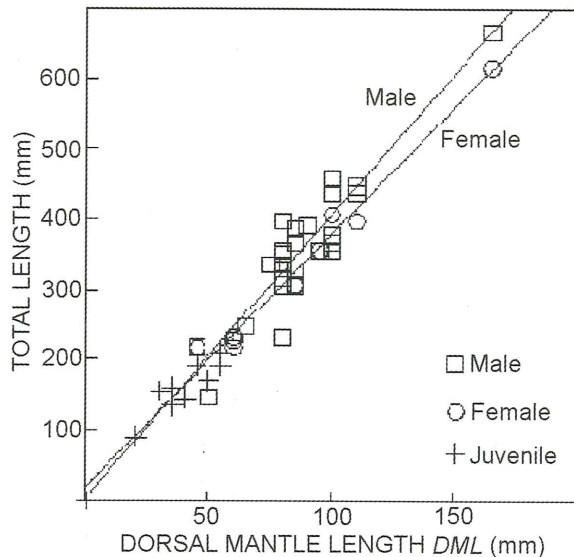


Fig. 1: Scatterplot of total length against dorsal mantle length (measurements taken from freshly dead material) for *Grimpoteuthis glacialis* collected on R. V. *Polarstern* Cruise ANT IV/2

Peninsula. One research component of the cruise was a fisheries survey using bottom trawls of commercial size (47 m headrope, 12 mm mesh codend liner). Sampling was conducted at 40 stations around Elephant Island, based on a stratified random survey design in depths to 500 m. A transect of stations at depths of 400, 600, and 800 m north-west of King George Island also was sampled twice with the same gear. The same transect was sampled with a large benthopelagic net (approximate mouth opening: 18 × 18 m, 12 mm mesh codend liner), fished day and night both very close to the bottom and higher in the water column. Additional bottom samples were collected at various depths between 98 and 3 213 m with an Agassiz beam-trawl (1 × 3 m mouth, 4 mm codend mesh), and a grid of stations was sampled both day and night with an RMT 1+8 midwater trawl.

All cephalopods were retrieved from all samples. Live cirrates were observed and photographed in aquaria. Prior to dissection, they were relaxed and killed in iced freshwater. Freshly dead material was used to measure dorsal mantle length (DML) and to determine sex and maturity. As described below, males were considered to be mature if sperm packets similar to the spermatophores described for *Opisthoteuthis* by Villanueva (1992) could be seen in the accessory sexual organs. Mature females had eggs in the oviduct.

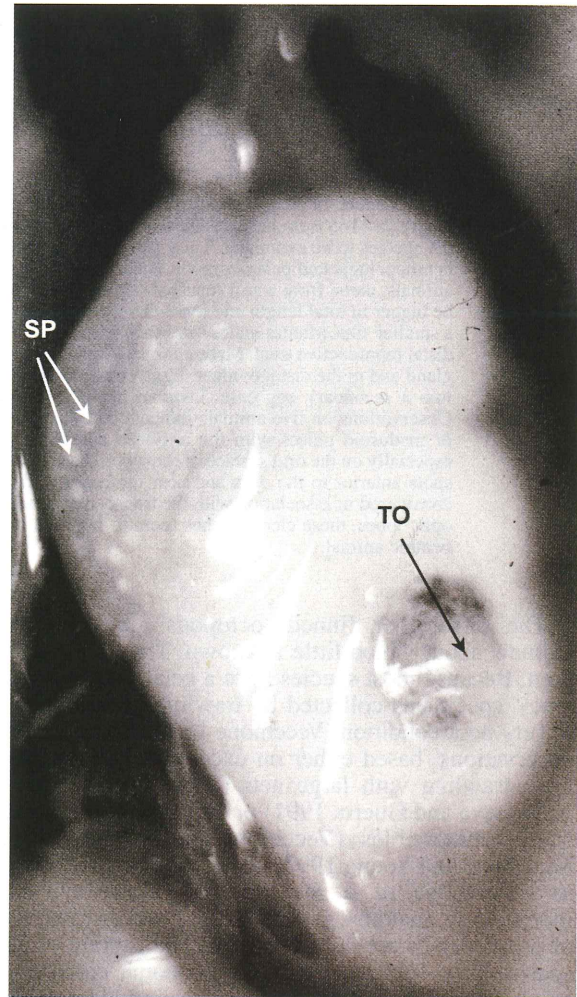


Fig. 2: Photograph of accessory reproductive organs of a mature male *Grimpoteuthis glacialis*, showing sperm packets (SP) and terminal organ (TO)

Immature animals of both sexes were those not meeting the criteria above, but whose sex could be distinguished macroscopically. Animals in which the sexual organs had not developed sufficiently for males to be separated from females were categorized as juveniles. Most specimens were weighed and total length was determined as well. Other observations, such as arm and fin lengths, sucker counts and sexual and other internal anatomy were recorded for small subsamples as time permitted.

Several very small specimens were fixed in 4%

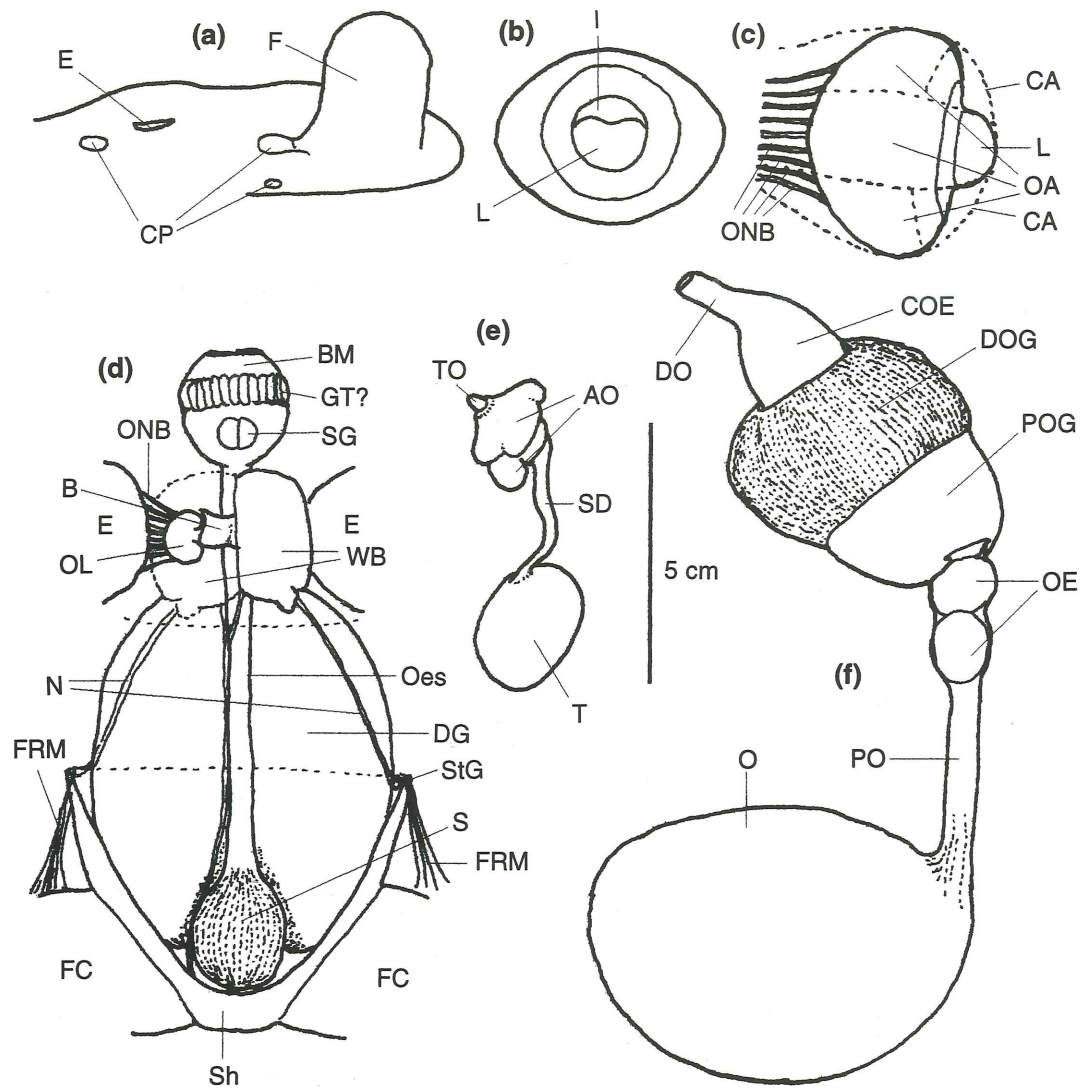


Fig. 3: (a) Lateral view of *Grimpoteuthis glacialis*, showing orientation of clear patches and eyes as the animal sits on the bottom, fin displaced upwards from normal resting position (see Fig. 5b); (b) Lateral view of eye, showing dorso-ventral compression; (c) Dorsal view of eye, showing optic nerve bundles inserted along the horizontal midline of the proximal surface of the eye, the outer capsule of muscle and connective tissue indicated by a dashed outline showing clear areas anterior and posterior to the lens; (d) Dorsal view of internal anatomy, the outer capsule of the eye and the dorsal white body removed on left side, dashed lines over the digestive gland showing the extent of the dorsal mantle cavity; (e) Male reproductive anatomy, ventral view; (f) Female reproductive anatomy, ventral view (Abbreviations – AO, accessory organs; B, brain; BM, buccal mass; CA, clear area; COE, coated oviducal egg; CP, clear patch; DG, digestive gland; DO, distal oviduct; DOG, distal oviducal gland; E, eye; Oes, oesophagus; F, fin; FC, fin cartilage; FRM, fin retractor muscles; GT?, glandular tissue?; I, iris; L, lens; N, nerve; O, ovary; OA, opaque area of muscle and connective tissue; OE, oviducal egg; OL, optic lobe; ONB, optic nerve bundle; PO, proximal oviduct; POG, proximal oviducal gland; S, stomach; SD, sperm duct; SG, salivary gland; Sh, shell; StG, stellate ganglion; T, testis; TO, terminal organ; WB, white body)

formaldehyde in seawater. Because of limited facilities aboard for formalin fixation of large animals, a mature male and female were frozen for subsequent fixation and archival as taxonomic vouchers after the conclusion of the cruise.

OBSERVATIONS

Grimpoteuthis glacialis was the only cirrate octopod collected. Although a few of the animals seemed to be more flaccid than average, no taxonomic characters could be found to distinguish them from the rest. All of the flaccid specimens were in poor condition and either were very small or came from longer than usual tows. It is therefore concluded that the flaccid condition resulted from net damage and that all cirrate specimens were conspecific.

Of 2 640 cephalopods collected during the cruise, 52 were *Grimpoteuthis glacialis*. All of those were collected by the large bottom trawl used for the fisheries survey. Size range was 20–165 mm *DML*, mean *DML* 79.3 mm, *SD* 31.8 mm and median *DML* 80 mm. Dorsal mantle length is the standard measurement of overall size for cephalopods, but for some octopods it is a small percentage of total length and can be extremely variable. For *G. glacialis*, *DML* appears to be a reliable indication of overall size because it exhibits a close linear relationship with total length throughout the size range examined (Fig. 1). Total length tended to be slightly longer in relation to *DML* for males than for females, although the difference is not statistically significant. Because the dorsal arms are the longest (arm formula I>II>III>IV), c. 2.6–2.8 times *DML* or 68–70 % of total length, this relationship also indicates low variability in length of the long dorsal arms.

Rather than the large complex spermatophores typical of most cephalopods, mature males of this species have tiny sperm packets superficially similar to the spermatophores described by Villanueva (1992) for the cirrate *Opisthoteuthis*. The sperm packets are found in the distal, or terminal, organs of the male reproductive tract (Fig. 2). Based on this criterion, 21 mature males were identified.

Only four mature females were collected. Mature females have a single oviduct with a huge oviducal gland, which approaches the size of the ovary (Fig. 3f). The numerous ovarian eggs vary greatly in size. A mature female (*DML* 110 mm, mass 1 170 g) had about 36 eggs of the largest size (10×16 mm) in her ovary along with many smaller eggs. The largest ovarian eggs were all characterized by longitudinal lines, probably equivalent to the follicular folds found

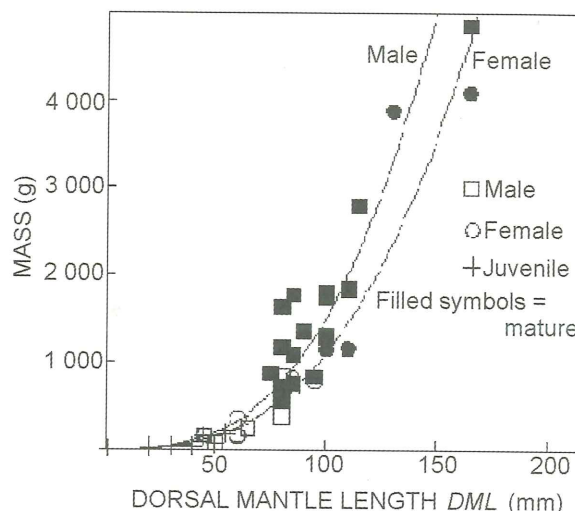


Fig. 4: Scatterplot of *Grimpoteuthis glacialis* mass against dorsal mantle length, with power curves fitted to show general trends in the data

on the ovarian eggs of incirrate octopods. Two eggs, also 10×16 mm but lacking the longitudinal lines, were found in the proximal oviduct near the oviducal gland. A single egg in the distal oviduct appeared to be larger (14×21 mm) but was covered with a thick sticky coating. After 10 minutes in seawater, the coating was no longer sticky, but cemented the egg firmly to the bottom of a plastic petri dish. When the coating was removed from the distal egg, it was the same size as eggs from the proximal oviduct. The colour of the viscous fluid inside the distal egg was light yellow; no embryonic development was noted. One egg was located inside the oviducal gland and also was coated with a secretion, presumably from the oviducal gland. The reproductive tract of another mature female (*DML* 130 mm, mass 3 880 g) was essentially the same as described above, except that the egg in the distal oviduct was slightly longer (14×22 mm) and the coating appeared to form a stalk, not homologous with the stalked chorion of incirrate octopods. Two smooth eggs were present in the proximal oviduct and one in the oviducal gland in addition to the one coated egg in the distal oviduct. Another female (*DML* 165 mm, mass 4 100 g) differed only in having six smooth eggs in the proximal oviduct.

Developing reproductive tracts are visible even in very small specimens, but the sex is not distinguishable without magnification at a *DML* less than c. 45 mm. Males appear to mature at a smaller size (75 mm *DML*) than females (100 mm *DML*). Sexual maturation seems

to be a period of rapid gain in mass, especially for males, which tend to outweigh females of similar size (Fig. 4). This disparity of mass is not just because males have greater total length. They also appear more robust, with thicker, more muscular arms. In the two largest specimens examined, which have the same *DML*, the diameter of the dorsal arms of the male is twice that of the female (60 v. 30 mm). Male arm length in this pair only exceeds that of the female by <6%.

The digestive tract of the animals generally matches the description given by Vecchione and Young (1997). Those authors did not locate the posterior salivary glands, but assumed them to be within the buccal mass, as has been reported for other species of *Grimpot euthis*. On a male of 100 mm *DML*, a ring of tissue that appeared to be glandular was observed on the buccal mass, anterior to what appear to be the anterior salivary glands (Fig. 3d). It is possible that this glandular tissue is homologous with the posterior salivary glands of other cephalopods, or it may be similar to the glandular tissue that Vecchione and Young (1997) found in the lips of the cirrate *Stauroteuthis syrtensis*.

A bilobed digestive gland has been suggested to be an important taxonomic character for cirrates (O'Shea, pers. comm.). The stomach sits in a depression in the dorsal posterior region of the digestive gland that makes this gland appear bilobed (Fig. 3d). However, internal indication of a bilobed structure to the digestive gland was not found. Beaks of five animals were examined and they differed from beaks examined by Kubodera and Okutani (1986) in that they were not "very weak and not fully chitinized". However, because the specimens described by Kubodera and Okutani (1986) came from a distant location, it is possible that the differences in beaks may represent variability between populations or species. The few stomachs that were opened either were empty or contained fragments of unidentified crustaceans.

The general colour of the animals was reddish-purple. Although the pigment is not organized into discrete chromatophores, colour pattern varied somewhat. On some live animals, the oral surface of the web was uniform in colour, slightly darker than the aboral surface. On others, the oral web pigment was concentrated onto the medial portion of each web segment, forming light and dark bands around the web (Fig. 5a). The colour of the suckers and cirri contrasted with that of the adjacent web, always lighter than the dark areas of the web but darker (cirri) or highlighted with darker surrounding tissue (suckers) than the light-coloured web bands. One individual, a mature male of 100 mm *DML*, had puckered the aboral skin on the arms, concentrating pigment into darker spots than the aboral web. Those dark spots were particularly prominent along the proximal $2/3$ of Arm Pairs III and

IV. The spots appeared to result from contraction of localized skin muscles.

Particularly noteworthy in the colouration of *Grimpot euthis glacialis* are paired discrete patches in the skin that appear superficially to be white spots (Fig. 5b). Although often overlooked in studies of cirrate morphology, such patches have been referred to (O'Shea pers. comm.) as "areolar spots." On closer examination, these patches proved to be transparent, i.e. devoid of pigment. The species has three pairs of these transparent skin patches, one anterior to the eyes, one at the anterior base of the fins, and a pair of smaller patches on the ventrolateral mantle located ventral to the patch at the fin base (Fig. 3a). The sizes of all patches varied, even among specimens of similar size. Because these clear patches might somehow be involved in photoreception, considerable time was devoted to dissection of fresh specimens, looking for potential extraocular photoreceptors associated with the location of the patches. No unambiguous evidence of any such receptors was found. The two pairs of patches on the mantle are dorsal and ventral to the location of the stellate ganglia, which in this species is at the anterior tips of the shell (Fig. 3d). Extraocular photoreceptors are unknown in cirrates, but in incirrate octopods they are located in the vicinity of the stellate ganglia (Fig. 3d). What appeared to be a second large ganglion was found in one specimen near the stellate, but it was not pigmented, as might be expected of a photoreceptor. Similarly, a nonpigmented ganglion on the aboral surface of Right Arm II was found beneath the patches anterior to the eyes on one specimen. No such ganglion was found on the left arm of that specimen or on any arm of any other specimen.

During the course of the dissections, an alternative hypothesis about the function of these clear skin patches was developed. When the animals are sitting on the bottom, as it is believed they do most of the time (see Discussion), the oral surface is downwards but the anterior-posterior axis of the head and mantle is parallel to the bottom. The clear patches anterior to the eye and at the base of the fin are on a horizontal plane with the eye (Fig. 3a). The eyes of *G. glacialis* are dorso-ventrally compressed and 33% longer on this horizontal plane than on the vertical, although the lens is spherical (Fig. 3b). Gaps in the muscles and connective tissue around the eye exist anterior and posterior to the lens (Fig. 3c). Unlike most octopods, the optic nerves of *G. glacialis* are organized into about nine bundles aligned along this same horizontal plane between the flattened eye and the flat, kidney-shaped optic lobe of the brain (Fig. 3c, d). Another peculiarity of the species is that the "white bodies" of the optic tract are joined to each other dorsal to the brain (Fig. 3d). The impression from this entire optic assemblage is

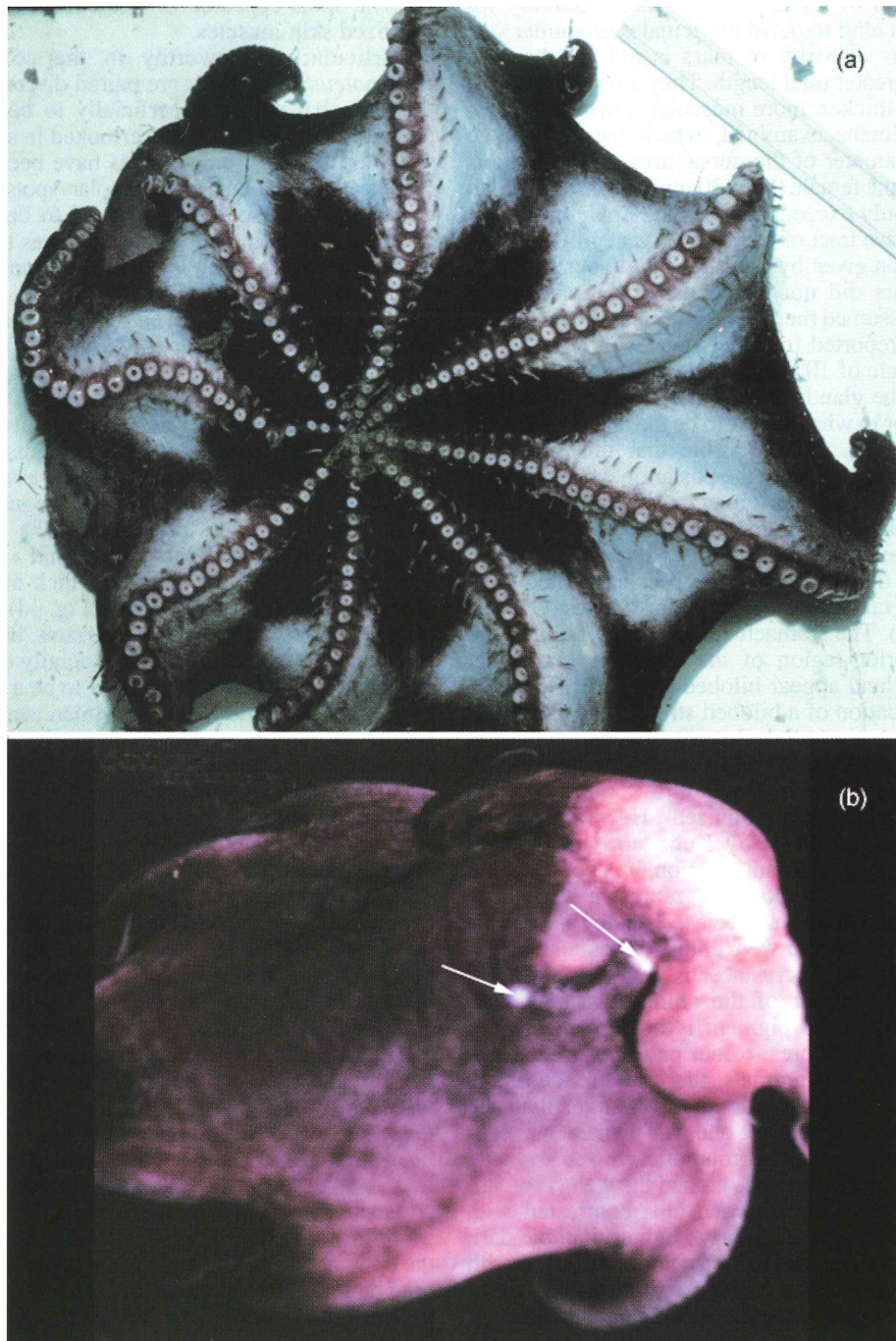


Fig. 5: Photographs of (a) oral surface of web on *Grimpoteuthis glacialis* with pigment concentrated to form dark and light bands, (b) dorsolateral surface of a live *G. glacialis* showing clear patches (arrows) in skin that appear to be white spots anterior to the eyes and at the bases of the fins

that the horizontal plane for the benthic animal is visually important. Cirrates, like many deep-sea octopods, are characterized by a thick subcutaneous layer of gelatinous consistency. On the fresh specimens that were dissected, this gelatinous layer was transparent. The transparent subcutaneous layer may allow light that enters on the horizontal plane through the clear skin patches to enter the eyes through the ocular muscle gaps and to be detected by the horizontally concentrated retina indicated by the optic nerve bundles.

Grimpoteuthis glacialis was collected at eight stations, ranging in depth from 333 to 879 m. Although pelagic and benthopelagic trawling was conducted at similar depths in the same geographic areas, cirrates were collected only by bottom trawl. Shallower water was sampled thoroughly with the bottom trawl, but bottom trawling at greater depths was conducted only with the much smaller Agassiz beam trawl. A single station accounted for 40 of the 52 specimens, where *G. glacialis* was dominant in the captured nekton both numerically and by mass. At that station, at a depth of 785 m, the net came up filled with soft grey mud. Of the 40 specimens, 17 were mature males, 2 were mature females, 5 were immature males, 7 were immature females and 9 were juveniles.

Several animals swam in shipboard aquaria. Swimming was strongly reminiscent of that described by Vecchione and Young (1997) for *Grimpoteuthis* sp. near Hawaii. It consisted solely of fin-flapping, resulting in posterior motion with the arms and web trailing behind. Neither mantle-jetting nor medusoid locomotion with the arm/web complex was seen. Occasionally, a small individual would hover by gently sculling with its fins for less than a minute while its arms and web were spread horizontally. After brief periods of swimming, the negatively buoyant animals would settle to the bottom with the arms and web spread downwards. Unlike the incirrate octopods observed during the cruise, none of these cirrates crawled in the aquaria.

DISCUSSION

The type locality for *Grimpoteuthis glacialis* is in the Palmer archipelago, near the present study area. The holotype was collected in a bottom trawl from a mud bottom 500 m deep. The current collections indicate that the type locality is indeed typical for the species. Because of the large number of shallow bottom trawls examined in which cephalopods, but not cirrates, were collected, *G. glacialis* probably does not usually venture into depths <333 m during the austral spring. However, it is impossible to infer a maximum depth

for the species based on the present collections. Although the deeper tows with the Agassiz trawl failed to collect them, these finned octopods might avoid the compressed mouth opening of such gear. A preference for mud bottoms is supported by the extraordinary number of specimens collected in a trawl that was completely clogged with mud. This is believed to be the largest reported single sample of cirrates ever taken. The patchy distribution of the current animals, with maximum abundance in a habitat that is difficult to sample, indicates that the species may be more abundant than previously thought.

As noted by Vecchione and Young (1997), the morphology of *G. glacialis* is consistent with a lifestyle similar to that of *Grimpoteuthis* sp. observed *in situ* near Hawaii. Such a lifestyle would be primarily benthic, with occasional short periods of swimming. The absence of *G. glacialis* specimens from large benthopelagic and pelagic trawls made at the same localities as collected in bottom trawls is consistent with a lifestyle that is primarily benthic.

Very little is known about the behaviour of cirrate octopods. Observations on the behaviour of animals that have been dredged up from the deep and confined in aquaria are, of course, suspect. However, a few tentative behavioural hypotheses are considered worthy of presentation here. *Grimpoteuthis glacialis* appears to depend almost entirely on its fins for locomotion. This is similar to the mode of locomotion of other species of *Grimpoteuthis* (Vecchione and Young 1997), but different from that of other cirrates, such as *Opisthoteuthis* (Pereyra 1965, Vecchione and Roper 1991), *Stauroteuthis* (Vecchione and Young 1997) and *Cirroteuthis* (R. Villanueva, Instituto de Ciencias del Mar, Barcelona, pers. comm. 1996). Furthermore, although the pigment of *G. glacialis* is not organized into the complex chromatophores used by other cephalopods to alter their appearance (Hanlon and Messenger 1996), this species seems capable of limited behavioural polymorphism. The most distinctive colour patterns found were on the oral surface of the web, but the ability to form darker spots along the aboral surfaces of the arms and perhaps to alter the size of the clear patches in the skin also seem noteworthy. Currently, however, it is not clear what is the functional significance of this polymorphism.

The clear patches in the skin are intriguing. They are not homologous with the white spots on other octopods, which are created by leucophores in the skin (Packard and Hochberg 1977). As noted by Vecchione and Roper (1991), similar clear patches are found in the cirrate genus *Opisthoteuthis*. In the latter genus, they are more extensive, forming rows along the aboral surfaces of the arms and extending onto the mantle. From the present research, the most likely

explanation for the clear patches is that they function as windows, allowing light to be transmitted through the transparent layer of subcutaneous gelatinous tissue to the eyes. In *G. glacialis*, this light-gathering capability seems concentrated in the horizontal plane of the benthic animal. It is possible that the clear patches in *Opisthoteuthis* function similarly, but that light from a greater variety of directions is so monitored. This function may be similar to that of the aphakic apertures used by deep-sea fish to gather the dim light of their environment without loss by image focusing (Munk 1966).

The reproductive biology of *G. glacialis* appears to be similar to that of *Opisthoteuthis* spp. as described by Villanueva (1992). Sexual development begins early and the period of maturity is prolonged. Males mature smaller, and therefore possibly earlier in the life cycle, than females. They also produce tiny sperm packets, rather than typical cephalopod spermatophores. The female reproductive tract is consistent with prolonged production of eggs. Females probably fertilize and lay eggs, either singly or in very small batches, over a long period of their lives. The eggs almost certainly are cemented to some substratum, perhaps by a secondary stalk formed from the coating of the oviducal gland. This is consistent with Boletzky's (1982) descriptions of unidentified cirrate eggs. It may be speculated that the larger, more robust morphology of the males may indicate some kind of agonistic competition for females; males are larger than females in other cephalopod species where there is such competition (Hanlon and Messenger 1996).

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